

The Journal of the Indian Botanical Society

(Formerly "The Journal of Indian Botany")

VOL. XXIX]

MAY, 1950

[No. 2

STUDIES IN CROP PHYSIOLOGY

Fertiliser Effects upon Water Relation of Potato Plant during Successive Stages of Soil Desiccation

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Introduction

Recent researches have shown that the ability of a plant to succeed well in an arid environment depends largely upon three set of conditions viz., (i) the rapidity with which the roots are capable of making good the losses during transpiration, (ii) the speed with which the conducting tract is capable of carrying upwards the absorbed water to different regions of shoot and (iii) the efficiency of the variety to restrict transpiratory losses from leaves. Where soil moisture is a limiting factor in crop production these three aspects of water relation deserve careful study specially when selection of a drought resistant strain is desired.

Another aspect that deserves equal attention is the role of fertilisers in bringing about alterations in water relation of plants. Experience has shown that application of manures and fertilisers improves the vegetative and reproductive vigour of plants but how far differences in growth behaviour are related to changes in water relation of plants is less understood. It is the intention to present in these pages relevant data concerning these aspects of the major problem of water relation of the potato plant.

Experimentation

The investigations were conducted on two varieties of Potato, viz., Katua and Phulwa during the cropping seasons of 1944-45 and 1945-46. Plants were grown in earthenware pots. Smaller pots with 5.5 kgm of soil were used during the first year of experiment while during the second larger pots filled with 10 kgm of farm soil (sandy loam) were utilised. In the first season both the varieties were sown while during the second, work was continued on only one variety, viz., Katua. The following

treatments with fertilisers were given to the two varieties in the year 1944-45 :

- T_1 .. No manure (Control)
 T_2 .. 5 gms. of sulphate of ammonia per pot.
 T_3 .. 10 gms. of sulphate of ammonia per pot.
 T_4 .. 15 gms. of sulphate of ammonia per pot.

Treatments were replicated three times. Fertilisers were dissolved in water and supplied to plants early in the life cycle soon after establishment. In all as many as 24 cultures were maintained in the first growing season.

In the second year, number of treatments were increased to eight combinations of N, P and K as under

$$\begin{array}{l}
 \left. \begin{array}{l} N \quad (Am. Sulph.) \\ N_0 = \text{No manure} \\ N_1 = 20 \text{ gms.} \end{array} \right\} \times \left\{ \begin{array}{l} P \quad (Cal. Phos.) \\ P_0 = \text{No manure} \\ P_1 = 8 \text{ gms.} \end{array} \right\} \times \left\{ \begin{array}{l} K \quad (Sulph. Potash) \\ K_0 = \text{No manure} \\ K_1 = 5 \text{ gms.} \end{array} \right\}
 \end{array}$$

Three pots per treatment were used. Fertilisers were added early in the growth cycle soon after establishment of young plant.

Plants belonging to different cultures were selected at random for the study of water loss during successive stages of soil desiccation. To start with each pot was supplied with adequate quantity of water so as to bring the moisture content in the vicinity of about 30 per cent on dry weight basis. Actual measurement of moisture content in soil was made by taking a requisite quantity of soil and drying it in an oven at 100°C till constant weight. Soil moisture was expressed as percentage of dry weight. The range in majority of cultures as estimated in this way varied between 28 and 30 per cent on dry weight basis.

Each experimental pot was removed to glass house at least a week before the start of the wilting experiment. Exposed soil and pot was coated with bees wax, paraffin and vaseline mixture in the proportion of 2 : 2 : 1. Care was taken to see that a perfect dry seal was secured. The hole at the bottom was carefully sealed so that net losses recorded could be attributed to be due to losses through the leaf surface only.

Twenty-four hours after sealing the pots, plants were weighed again, and the losses during twenty four hours' interval were recorded at various stages of desiccation. When permanent wilting was indicated, *i.e.*, when drooping leaves failed to recover to the normal stage even on exposure to saturated conditions of humidity at night, the moisture content was determined as before. Percentage of un-available moisture on oven dry weight basis was thus determined by direct experiment.

Transpiration loss during twenty-four hours' interval in each culture was calculated on the basis of unit dry weight of roots, shoot and tubers in the first year of experiment and on unit dry weight of shoot only during the second year. As will be observed, potato plants at an average survived for a period of 10 to 15 days. Towards the end of this period weight of component organs was recorded. Wilting experiments were carried out at three stages of growth in the first year and at one stage only in the following season.

Regular records of atmospheric temperature, humidity and wind velocity during the period of experimentation were simultaneously kept for evaluating the extent to which the intensities of environmental factors singly or jointly affected the rate of transpiration.

Experimental Findings

A. TRANSPIRATION LOSSES DURING EARLY STAGES OF GROWTH (30 DAYS) OF PHULWA AND KATUA VARIETIES

Transpiration per plant: Data recorded on transpiration losses per plant on each day of experiment (Figs. 1, 2) showed certain characteristic features of the two varieties. During the first four days the fluctuations in transpiration per plant in both varieties were most marked. Between the fifth and ninth day, transpiration reached more or less a level phase. On the 10th day a sudden increase in transpiration was again recorded. That was soon followed by a fall which reached a low level on the 12th day of wilting experiment. The last phase prior to permanent wilting was again characterised by a level phase of water loss which almost touched the zero level in both the varieties under experimentation.

Treatment with nitrogen did not alter the sequence of changes in transpiration. Differences between individual treatments were more marked during the first fluctuating phase of transpiration and were noticeable for four days. In the second, third and fourth phases of transpiration, the differences were less discernible. Irrespective of treatments under which plants grew, a rejuvenation of transpiratory activity was noted prior to fourth stage of temporary wilting (Figs. 1, 2). This was true for both the varieties under investigation.

Transpiration per unit dry weight of roots: When expressed in terms of unit weight of roots, transpiration showed the above four phases viz., (i) fluctuating phase between 1-4 days, (ii) level phase between 5-9 days, (iii) rejuvenation phase between 9-12 days and (iv) stationary phase of very low transpiration between 12-15 days of experiment. Differences due to treatments were less evident in Katua variety (Table 1) but more marked in Phulwa variety.

Transpiration per unit dry weight of shoot: Expressed in terms of the weight of shoot, transpiration in Phulwa showed fluctuations similar to those noted in case of transpiration per unit dry weight of root or entire plant. In the present case, control plants (without any nitrogen) exhibited a higher transpiration rate than other Phulwa plants treated with varying levels of nitrogen. Differences between the control and the treated plants were noted during the first, second and third phases of desiccation. Levels of nitrogen were without appreciable effect during the later stages (II, III and IV phases) but were more evident during I phase (Table 2). In case of Katua again, control plants showed the general tendency of higher rate of transpiration per unit weight of shoot than other plants treated with varying levels of nitrogen. Differences due to different levels of nitrogen were once again noticed during the fluctuating phase more than during other phases of desiccation.

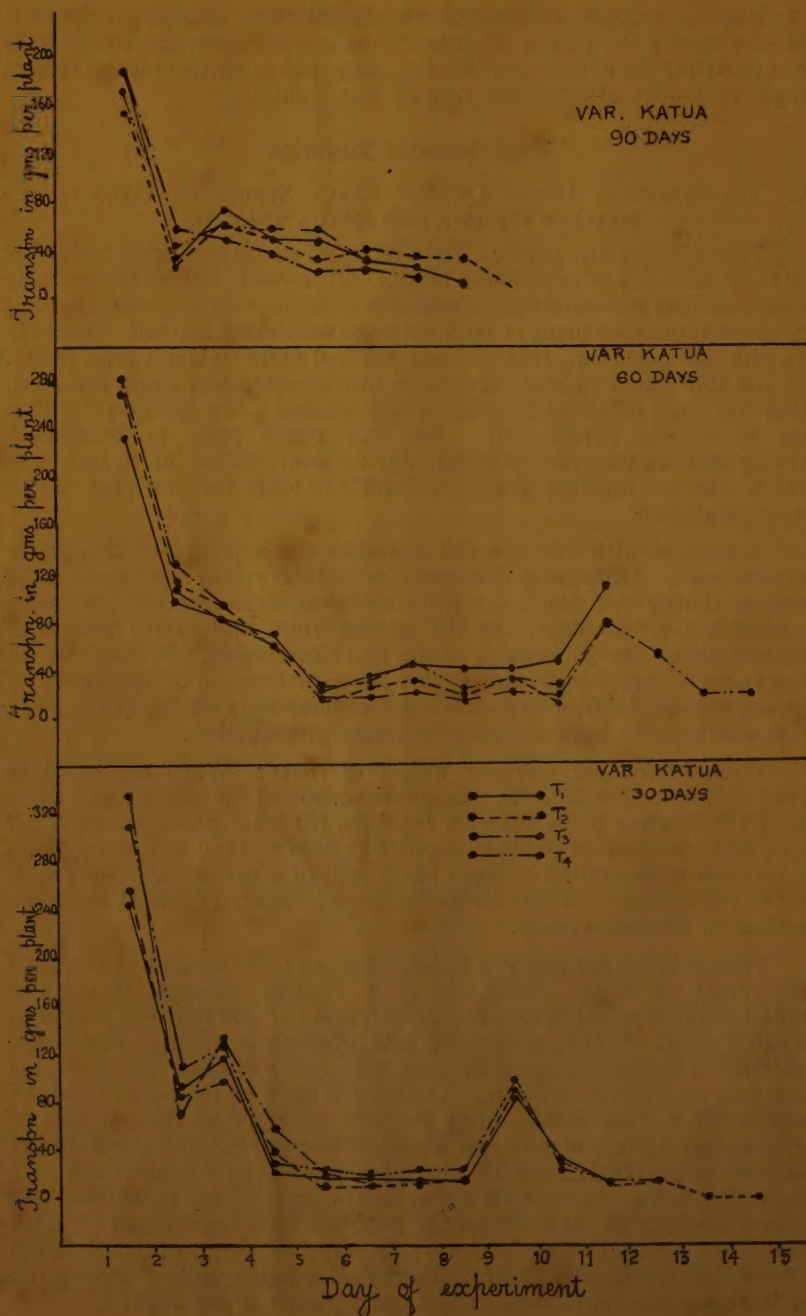


Fig. 1.—Effect of different levels of nitrogen on transpiration loss per plant (Var. Katua) at different stages of soil desiccation.

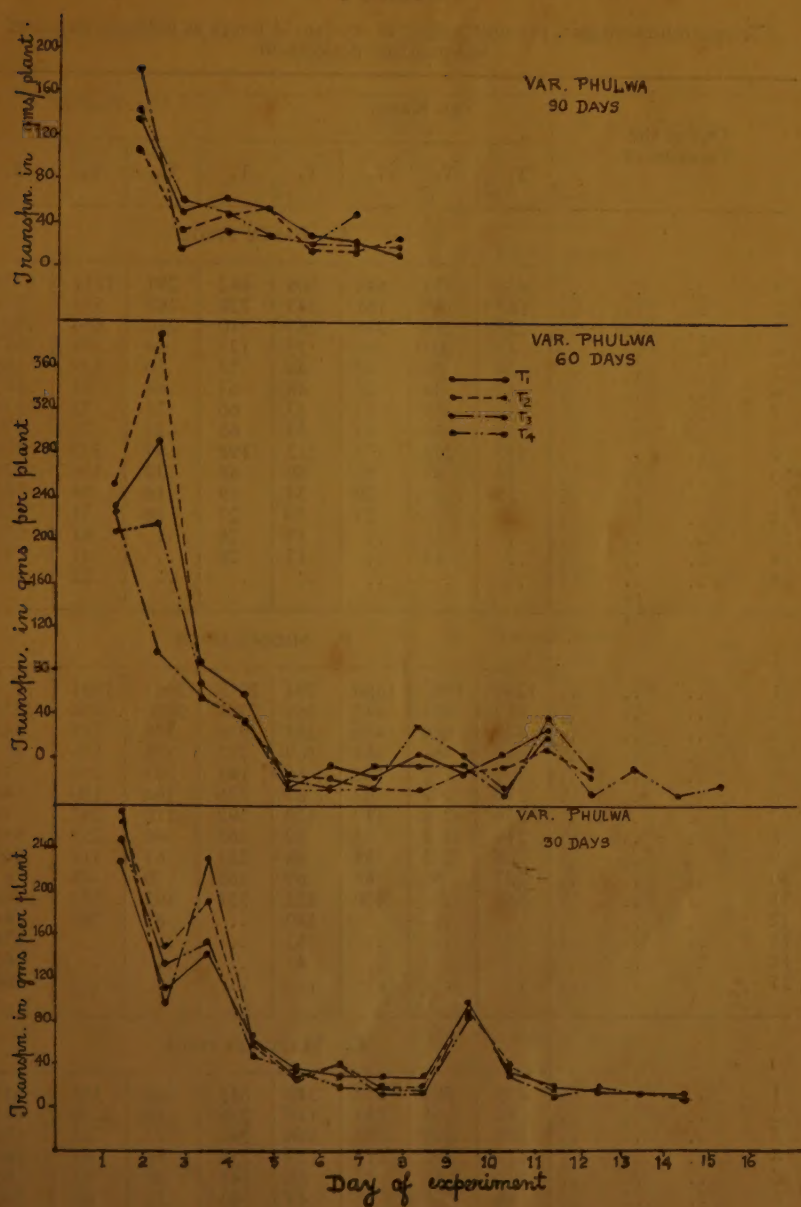


Fig. 2.—Effect of different levels of nitrogen on transpiration per plant (Var. Phulwa) at different stages of soil desiccation.

Table 1

Transpiration in gms. per unit weight of root in 24 hours at different stages of soil moisture desiccation.

Day of the Experiment				Var. Katua				Var. Phulwa			
				T ₁	T ₂	T ₃	T ₄	T ₁	T ₂	T ₃	T ₄
A. EARLY STAGE											
1	453	374	648	708	482	291	1111	1776
2	167	180	161	245	228	165	532	938
3	221	259	245	283	310	210	634	1100
4	47	101	112	75	133	56	198	347
5	34	34	40	48	74	30	129	226
6	33	34	26	46	63	44	83	145
7	31	39	33	53	60	21	73	130
8	31	39	33	53	60	21	73	130
9	153	228	175	212	192	97	335	586
10	36	85	59	60	68	39	136	238
11	25	29	29	34	39	16	54	95
12	28	36	27	39	27	16	71	124
13	19	..	17	26	..	41	71
14	19	..	17	26	..	41	71
15	32	..
B. MIDDLE STAGE											
1	1240	1940	1680	794	2079	2061	1841	1174
2	517	833	647	361	2501	3090	974	1221
3	429	640	476	231	976	776	715	543
4	368	431	355	169	772	578	536	373
5	107	102	102	66	141	202	154	78
6	170	172	92	87	276	164	150	86
7	216	214	117	120	192	110	242	78
8	214	118	73	59	365	46	258	352
9	208	243	138	98	223	61	314	205
10	247	50	68	69	365	70	48	67
11	568	..	450	222	538	102	552	469
12	140	..	61	207	48
13	52	176
14	41	62
15	104
C. MATURITY STAGE											
1	439	304	554	342	615	160	323	427
2	84	61	134	119	236	56	36	193
3	174	129	101	146	292	77	67	116
4	123	102	117	129	255	84	61	108
5	121	69	81	66	141	30	51	86
6	85	78	78	49	63	21	41	386
7	64	89	63	38	32	37	90	..
8	38	62	22
9	17

Table 2

Transpiration in gms. per unit dry weight of shoot at different stages of soil moisture desiccation.

Day of the Experiment				Var. Katua				Var. Phulwa			
				T ₁	T ₂	T ₃	T ₄	T ₁	T ₂	T ₃	T ₄
A. EARLY STAGE											
1	1747	162	272	148	438	274	234	275
2	643	432	674	514	206	156	83	146
3	854	624	103	593	280	199	200	171
4	181	242	470	157	120	53	51	54
5	133	82	17	10	67	28	24	35
6	129	8	11	10	57	42	33	23
7	119	9	13	11	54	20	14	20
8
9	590	55	73	44	174	92	80	91
10	254	20	25	13	62	37	27	37
11	95	7	12	7	35	16	10	15
12	107	9	11	8	33	16	19	19
13	7	..	3	24	..	11	12
14	7	..	3	24	..	11	12
B. MIDDLE STAGE											
1	736	85	73	471	520	89	61	117
2	306	36	28	214	640	133	32	122
3	255	28	23	137	244	33	23	54
4	219	19	16	100	193	23	18	37
5	63	4	4	39	35	9	5	8
6	101	8	4	52	91	7	5	9
7	128	9	5	71	55	5	8	8
8	126	6	3	35	91	4	9	35
9	124	11	6	58	13	9	4	20
10	147	2	3	41	91	11	2	7
11	337	..	19	131	134	10	18	3
12	83	..	8	7	5
13	32	18
14	23	6
15	10
C. MATURITY STAGE											
1	56	221	226	136	398	64	46	73
2	11	44	55	48	153	23	5	33
3	22	94	62	58	189	31	10	28
4	16	74	48	45	165	34	9	18
5	15	50	33	26	91	12	7	15
6	11	57	32	20	87	12	7	27
7	8	47	38	15	45	20	6	..
8	5	45	9
9	12

B. TRANSPIRATION ON SUCCESSIVE DAYS OF SOIL DESICCATION DURING MIDDLE PORTION OF AGE CYCLE (60 DAYS).

During the middle portion of life cycle of potato, transpiration per plant exhibited marked fluctuations with advance in the period of soil desiccation. In early stages (1-5 days) of the progress of experiment, plants showed a high rate of water loss. Variations due to treatments were more marked in case of Phulwa than in case of Katua. The second and third phases so characteristically noted during early life cycle were less distinct during this period. Temporary wilting was noted from 7-11 days in case of Katua and 7-12 days in case of Phulwa. Stationary and rejuvenation phases prior to wilting were more or less intermingled with the result that transpiration during that period (6-12 days) started with a low value and gradually rose to a climax on the 12th day. Permanent wilting was noted on 12th and subsequent days depending upon treatments given to the plants. During the last phase, transpiration again fell down to zero level in both the varieties with ultimate drying of plant. This was true for both the varieties (Figs. 1, 2).

Transpiration per unit dry weight of roots: Losses per unit dry weight of root again showed three distinct phases (i) between 1-5 days II and III between 6-11 days and IV after 12 days. Treatments with nitrogen were more effective during early stages of 1-5 days. Milder doses of nitrogen were found to increase transpiration more than heavier doses. In the second and third stages, no-nitrogen plants transpired more than plants treated with higher doses of nitrogen. Permanent wilting was again preceded by rejuvenation of transpiratory activity followed by a decline. This was true for both Katua and Phulwa varieties (Table 1); in the latter case control plants tended to show a higher transpiration for most of the phases of desiccation.

Transpiration per unit dry weight of shoot: Expressed per unit dry weight of shoot, transpiration of control plants exhibited distinctly higher value than that of nitrogen treated ones in case of both the varieties (Table 2). In the first case differences due to treatments with increasing levels were evident more than in the second variety. The general tendency was, however, the same as that recorded for transpiration per unit dry weight of root.

Transpiration per unit weight of tuber: The variations in transpiration per unit dry weight of tubers were more evident in case of Phulwa than in case of Katua particularly during the first nine days of the commencement of experiment. During second and third phases, control Phulwa plants showed distinctly higher transpiration than other nitrogen treated plants. This was not so evident in case of Katua variety (Table 3).

C. TRANSPIRATION ON SUCCESSIVE DAYS OF SOIL DESICCATION DURING MATURITY PERIOD OF POTATO (90 DAYS).

Total transpiration per plant: Compared to earlier stages of life cycle, losses during transpiration at this period showed only two distinct phases (Figs. 1, 2). During the first phase lasting for 3 days, there was a distinct fall in transpiration per plant, irrespective of either the varieties or the treatments given to the plants. The second, third and fourth

Table 3

Transpiration/dry weight of tubers at different stages of desiccation.

Day of the Experiment				Var. Katua				Var. Phulwa			
				T ₁	T ₂	T ₃	T ₄	T ₁	T ₂	T ₃	T ₄
A. MIDDLE STAGE											
1	874	826	422	380	1048	916
2	321	220	105	132	370	484
3	427	318	160	152	892	570
4	90	124	73	40	229	180
5	66	42	26	26	108	117
6	64	42	17	25	149	75
7	60	48	21	29	63	66
8	60	279	21	28	63	66
9	295	104	114	114	356	304
10	127	32	38	32	119	49
11	48	44	19	19	45	49
12	53	24	18	21	83	65
13	24	..	9	48	37
14	9	48	37
15	3	..
B. MATURITY STAGE											
1	166	367	248	331	1247	1387	445	404
2	69	158	96	150	1585	2060	235	421
3	57	121	70	96	605	517	173	187
4	49	81	52	70	476	358	129	128
5	14	19	15	27	87	134	37	27
6	23	32	14	36	171	110	36	29
7	29	41	17	50	119	74	58	27
8	28	14	11	25	226	67	63	121
9	20	46	19	41	138	143	76	70
10	33	9	10	19	226	176	11	23
11	76	..	66	92	333	252	133	107
12	59	..	119	50	16
13	21	61
14	16	21
15	36

phases noted during earlier period of the life cycle appeared to be indistinct. The last three phases more or less merged into one phase, characterised by a relatively high transpiration on fourth day and gradually falling down to zero level on the tenth day. The effects of treatments in bringing about any alteration in the trend of variations were more or less insignificant. Temporary wilting commenced on the fifth day in certain treatments (Control) ; in others it was noted a little later.

Transpiration per unit dry weight of root : This also followed the same trend of variation as those recorded for total transpiration per plant. The second, third and fourth phases of transpiration were not as distinct

as during early periods. The treatments were more effective in case of Phulwa than in case of Katua. In the first case, control plants during 1-9 days showed higher transpiration than other nitrogen treated plants. In Katua no marked differences were recorded (Table 1).

Transpiration per unit dry weight of shoot: Expressed per unit dry weight of shoot, transpiration in general, showed a decline with progress of wilting. The first phase lasted for 2 days, the II, III, and IV phases were not at all distinct (Table 2). In control Phulwa, plants showed higher transpiration than other nitrogen treated ones. In Katua, the reverse was the case; control plants exhibited lower transpiration than other nitrogen treated plants.

Transpiration per unit dry weight of tuber: Transpiration calculated on dry weight basis of tubers showed lesser differences with treatments in both the varieties (Table 3). A fairly low rate of transpiration was recorded for the varieties on successive days. Different phases noted so characteristically during earlier stages, were indistinct. The general tendency of treatments was to exhibit a low rate of transpiration with the progress of desiccation.

D. TOTAL TRANSPIRATION/DRY WEIGHT RATIO AT SUCCESSIVE STAGES OF DESICCATION IN RELATION TO ENVIRONMENTAL CONDITIONS.

Early period of life cycle (30 days): When transpiration per plant was divided by the dry weight at successive stages of desiccation the ratio was found to vary characteristically. All the four stages observed previously have been noted. Thus, during the first five days irrespective of treatments given to plants the ratio was high. In case of Katua, the ratio was higher under no manure. The differences in Phulwa during this period were less evident under different treatments.

Between the fifth and ninth days the ratio of transpiration to dry weight of entire plant fell down to a level value; no marked differences due to treatments were noted (Fig. 3). This was true for both the varieties under experimentation. Between ninth and twelfth day, slight rejuvenation of transpiration was noticed in both the varieties more so under no-nitrogen treated plants (T_1) than under other fertiliser treatments. The stage of permanent wilting was characterised by a very low rate of transpiration under all treatments and varieties. No relation between transpiration and atmospheric temperature, humidity or wind velocity was evident during early stage of life cycle (Fig. 3).

Middle period of life cycle (60 days): In the middle portion of the life cycle treatment effects were still less evident in Katua. In Phulwa, control plants showed higher ratio at all stages than treated ones. All the four stages were again noted. The first fluctuating phase was more evident in Phulwa than in case of Katua. Partial increase in transpiration towards wilting was noted in both varieties. Control plants showed higher transpiration specially in Phulwa. Environmental factors again did not show any rigid relation with transpiration drift (Fig. 4).

Maturity stage of life cycle (90 days): Towards the approach of maturity, transpiration/dry weight ratio showed practically no phasic rise even during the first and third stages of progress of desiccation.

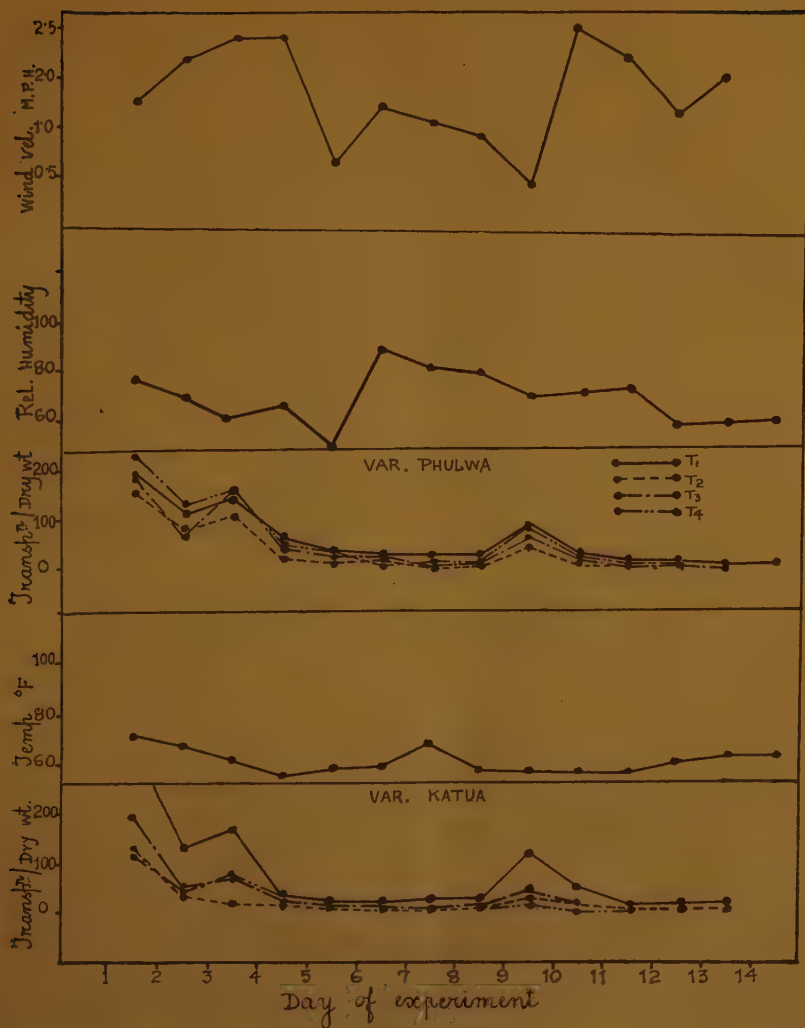


Fig. 3.—Transpiration per unit dry weight in relation to N-doses soil moisture desiccation and climatic conditions (30 days).

Treatment effects were practically (Fig. 5) insignificant. Here again environmental factors showed no relation with march of this ratio.

E. EFFECTS OF N, P AND K UPON TRANSPIRATION

Transpiration per plant: In the second year of investigation the effect of treatments on transpiration was again less significant than the effect of depleting soil moisture. Irrespective of the treatments, there was noted a general decline with advance in desiccation. The fluctuating

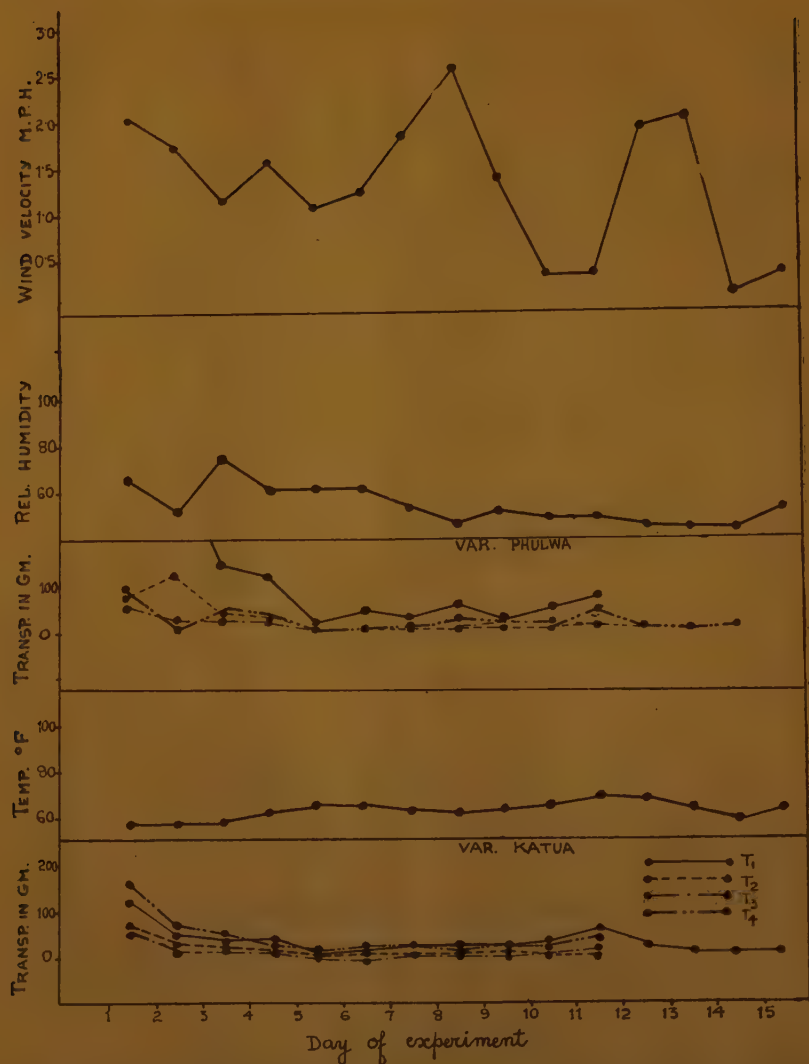


Fig. 4.—Transpiration per unit dry weight of plants in relation to N-doses soil moisture desiccation and climatic conditions (60 days).

phase extended between 1-14 days of the experiment. The second declining phase of transpiratory activity, was observed between fourteenth and eighteenth day. Except in case of control, where transpiration during the second phase reached a very low level, other treatments showed a relatively higher rate (Fig. 6). During the third phase, all fertiliser treated plants showed an increase in activity to be soon followed by

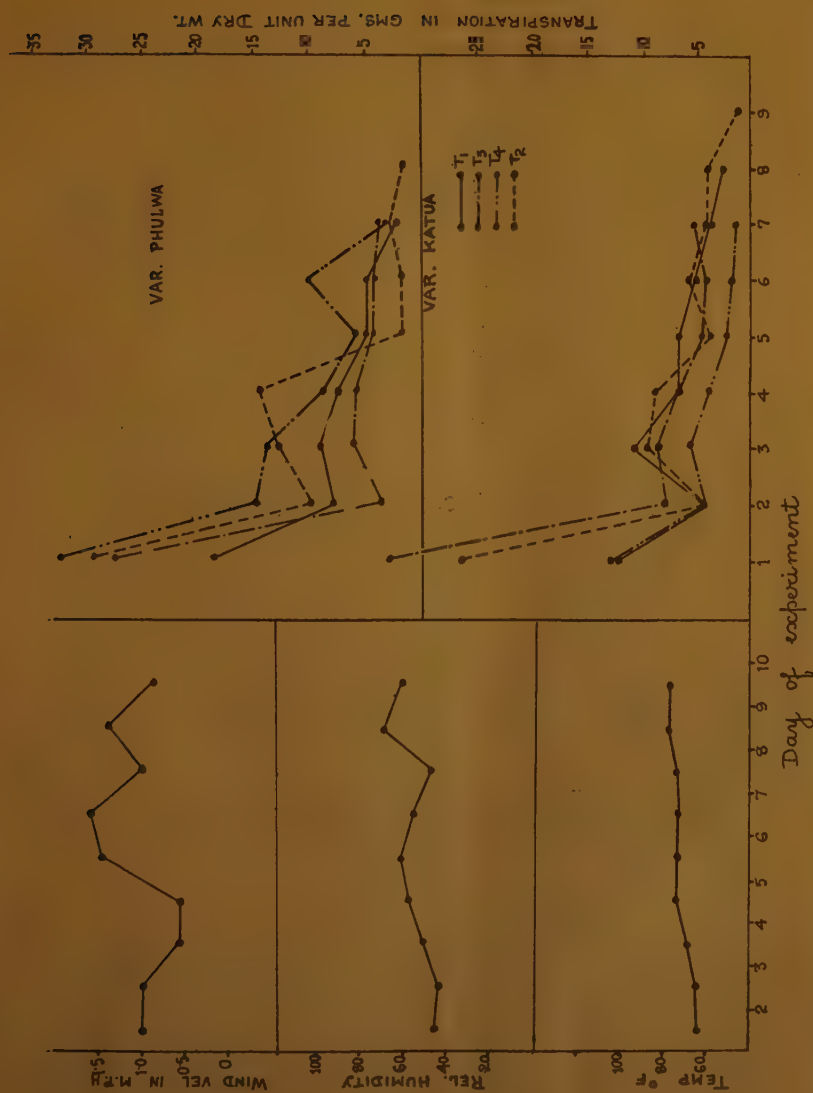


Fig. 5.—Transpiration per unit dry weight of plants in relation to nitrogen doses, soil moisture desiccation and climatic conditions (90 days).

cessation of water loss. Tendency to exhibit another maximum at permanent wilting was also noticed. Treatment differences, however, were less distinct at all phases of desiccation.

Transpiration/shoot dry weight ratio: Transpiration/shoot weight ratio again followed the same trend of variation as indicated above. Fertilisers raised this ratio at all stages of desiccation. Maximum effect was noticed in plants treated with nitrogen, where this ratio showed the maximum value (Fig. 7). NPK treated plants also showed marked increase over NP, NK, and PK treated plants. The second phase of stationary transpiration was more characteristic in control than in other treatments where fluctuations were more apparent. Increases in this ratio during phase of temporary wilting (at or prior to wilting) were observed (Fig. 6 and 7). No relation between environmental factors and intensity of transpiration per unit dry weight of shoot was recorded.

F. TOTAL TRANSPIRATION/DRY WEIGHT RATIO IN RELATION TO AGE AND FERTILISER TREATMENTS

Total loss of water during the entire period of experiment when the plant changed from a state of complete turgescence to wilting, was divided by the total dry weight of plants at wilting. This value varied both with treatment and the age of plants (Table 4). In Phulwa this ratio fell off with age in majority of treatments. Control plants showed the highest water loss per unit dry weight during the first two stages only. At the third, the effect of first dose of nitrogen (T_2) was more prominent in raising this ratio. The higher the nitrogen level the greater was the total water/dry weight ratio during the duration of desiccation.

No consistency in effect was noted at all stages in case of Katua variety. Treatment with nitrogen showed different effects at different periods. Control plants in general showed higher ratio during early stages only (Table 4).

Fertilisers, in general, increased transpiration per unit dry weight at different phases of desiccation. Nitrogen treated plants showed highest water loss; NPK treated ones were next in order and K treated plants showed the least amount of water lost (Table 5).

G. WILTING COEFFICIENT

Wilting coefficient of soil ranged between 4.2 to 8.1 at different stages of life cycle in case of Katua and between 4.3 to 7.1 under different treatments in case of Phulwa. The effect of treatment on the age of the plant was not consistently similar in the two varieties (Table 6). In the second year, nitrogen treated plants depleted soil moisture to the maximum extent. Next in order were the P treated plants; K and PK treated potato reduced soil moisture to a relatively lesser extent than other treatments. Wilting coefficient varied slightly with fertilisers and the extent of variation ranged between 3.6 to 7.5 for the different treatments.

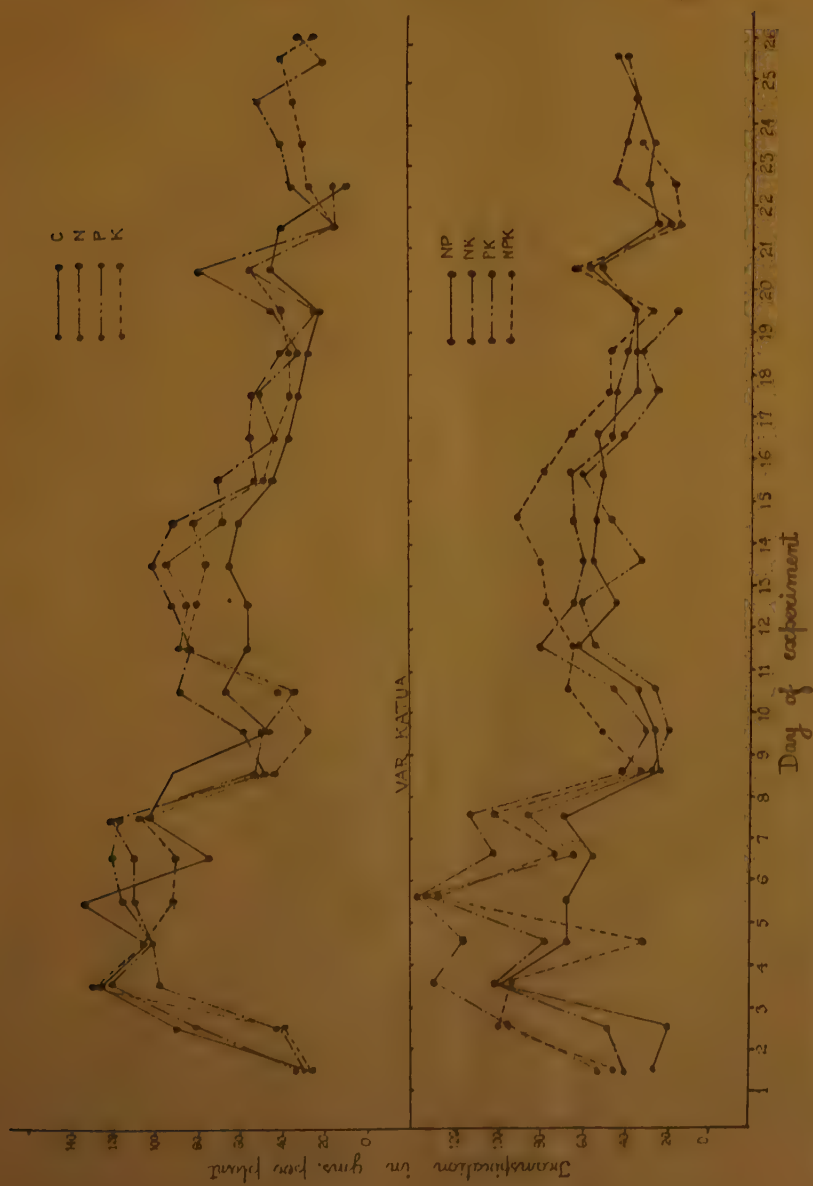


Fig. 6.—Transpiration per plant in relation to fertiliser treatment and soil moisture desiccation.

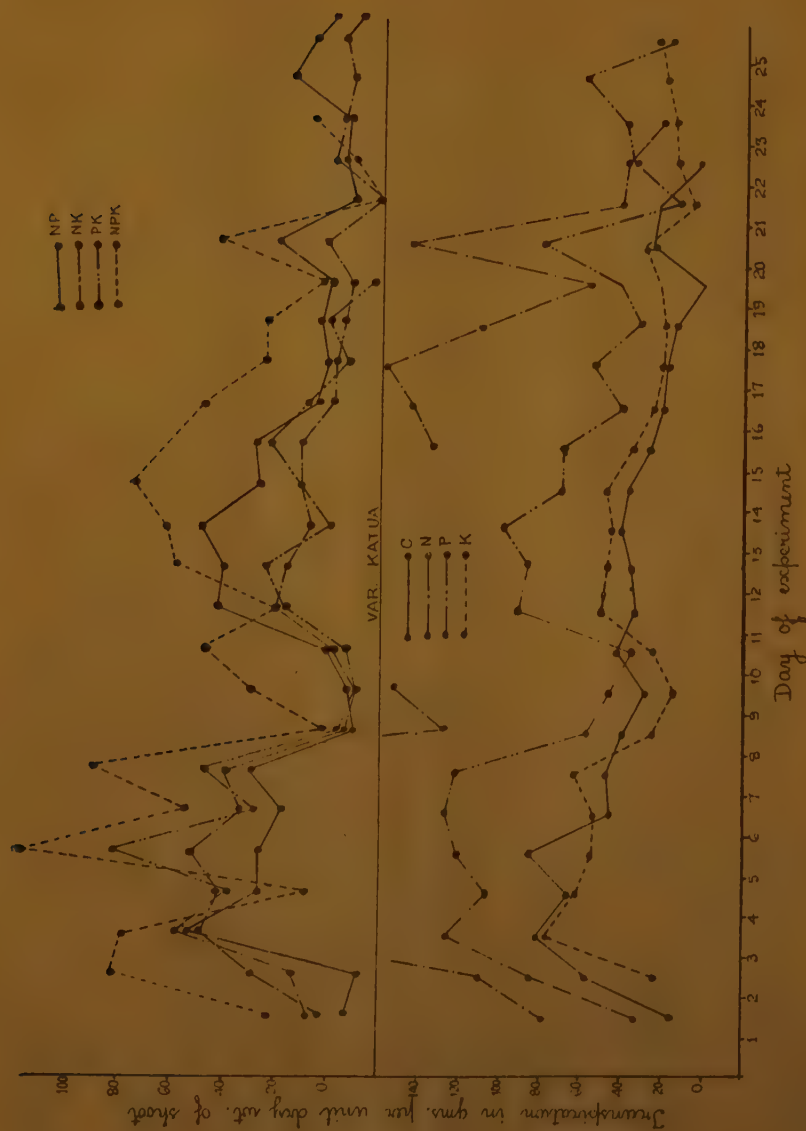


Fig. 7.—Transpiration per unit weight of shoot in relation to fertilisers and soil moisture desiccation.

Table 4

Transpiration/Dry weight ratio at different stages in life cycle (1944-45).

A. VARIETY : PHULWA

Stage of life cycle	Characters	T ₁	T ₂	T ₃	T ₄
Early (30 days)	Total Transpiration (1-15 days).	797	881	831	781
	Dry weight of plant Transp./Dry weight	0.99 805	1.85 476	1.40 593	1.00 781
Middle (60 days)	Total Transpiration (1-15 days).	989	464	893	960
	Dry weight of plant Transp./Dry weight	0.86 115	3.61 128	5.10 175	2.90 325
Maturity (90 days)	Total Transpiration (1-9 days).	267	887	329	234
	Dry weight of plant Transp./Dry weight	2.21 121	3.32 270	6.80 41	4.51 52

B. VARIETY : KATUA

Early (30 days)	Total Transpiration (1-15 days).	644	621	664	324
	Dry weight of plant Transp./Dry weight	0.68 947	1.96 376	1.76 371	2.45 132
Middle (60 days)	Total Transpiration (1-15 days).	659	672	607	959
	Dry weight of plant Transp./Dry weight	1.93 394	4.1 164	5.3 114	1.78 539
Maturity (90 days)	Total Transpiration (1-9 days).	360	471	393	653
	Dry weight of plant Transp./Dry weight	7.77 47.8	7.88 59.8	6.15 63.8	14.97 43.7

Discussion

Data recorded in the previous pages bring certain facts to prominence regarding the behaviour of a fully turgescient potato plant during soil desiccation. If the views developed by Shull (2) were to be taken into consideration, the entire process of change from full turgidity to wilting may be pictured as follows :

The plant body, consisting of a mass of organic colloidal materials, inorganic ions and molecules and organic substances in solution, forms a hydration link between the vapour phase of moisture in the atmosphere

Table 5

Transpiration/Dry weight ratio at 67 days in life cycle (1945-46).

VARIETY : KATUA

Treatments	Total loss of water	Dry weight of plant	$\frac{\text{Transpiration}}{\text{Dry weight}}$
C ..	1351	1.54	877
N ..	1440	0.38	3789
P ..	1637	0.95	1733
K ..	1442	1.62	890
NP ..	1154	0.93	1240
NK ..	1590	1.29	1232
PK ..	972	0.89	1092
NPK ..	1307	0.68	1922

Table 6

Wilting Coefficient of soil at different stages of life cycle (1944-45)

Stages			Variety : Katua				Variety : Phulwa			
			T ₁	T ₂	T ₃	T ₄	T ₁	T ₂	T ₃	T ₄
Early	6.3	7.6	5.8	6.3	6.4	6.7	5.6	6.0
Middle	8.1	7.2	7.1	6.3	6.3	7.1	4.2	5.1
Maturity	5.6	4.6	5.1	4.2	5.2	5.3	6.1	4.3

Table 7

Wilting Coefficient of soil under different fertilisers (1945-46)

VARIETY : KATUA

Fertilisers	Wilting coefficient
C	5.6
N	3.8
P	4.5
K	6.5
NP	5.3
NK	5.3
PK	7.5
NPK	5.3

and both liquid and vapour phases in the soil. Under normal conditions of water supply when the cells are usually swollen, the forces with which water is retained in the cell, are relatively less than when the cells are in a state of plasmolysis. Under former conditions, increasing stresses of the atmosphere are able to help in accentuating losses of moisture during transpiration. The plant loses water at fluctuating rates till the moisture content of the plant body is reduced to a certain critical limit under adverse conditions of soil moisture. When this is so, considerable colloidal forces develop inside the plant body as a result of which the losses during transpiration considerably fall down to a low stationary level. This condition is characteristic of the second phase of the desiccation experiments narrated in the previous pages.

With adverse soil moisture conditions still persisting, as in the investigations herein described, further losses of water reduce the moisture content of the plant body to limits lower than the critical concentration desirable for maintaining normal colloidal and other properties of the cell. Under such conditions when further absorption from the soil is not possible and when the atmospheric conditions still persist in withdrawing water from the plant body against huge forces, the plant colloids and protoplasm lose their power of resistance. When complete loss of protoplasmic control of this physiological processes is attained, the pressure with which moisture is retained in the plant body is suddenly released. Sudden increase in transpiratory activity takes place under such conditions though only for a very short duration. This is what has been observed to take place during the third phase of desiccation.

Sooner or later the tissues get too dry to carry on their normal processes of metabolism and the plant shows permanent wilting as was evident during the course of these investigations at the fourth stage of desiccation.

Results obtained further point out that this sequence of changes is characteristic of the two varieties, and is not to any considerable extent affected by treatment with fertilisers. At earlier stages, however, the different phases of desiccation are more prominently observed than at later periods of the life cycle. As a rule the no manure plants show higher transpiration during earlier stages of desiccation but this difference gradually becomes insignificant when the soil moisture is depleted below a certain critical limit. In its essential details the effects noted are more or less identical to those recorded earlier in case of turmeric (1) and wheat (3) plants.

Irrespective of both these factors of soil moisture and fertilisers, potato plants depleted soil moisture to more or less the same limit under different conditions. This is shown by more or less similar range of wilting coefficient for the two varieties of Phulwa and Katua, the lower limit in both these varieties remaining more or less same at different periods of life cycle. Fertilisers affect wilting coefficient to a small extent; nitrogen fed plants deplete soil moisture most. Wilting coefficient in consequence is lowest in nitrogen treated soils than in others. Phosphorus treated soils followed next in order.

Summary

The paper deals with the water relation of potato plant during the process of soil desiccation. Experiments were conducted on two varieties. Simultaneous effect of fertilisers was also investigated at successive stages of life cycle.

In general transpiration drifts with desiccation of soil showed four such phases, viz., (i) the fluctuating phase of high transpiration rate when soil and atmospheric factors largely determined water loss ; (ii) the level phase of transpiration when internal colloidal and other forces determined transpiration ; (iii) the phase of temporary high transpiratory activity lasting for a short duration during the prewilting stage when internal forces regulating the extent of water loss were unable to keep control over the physiological behaviour of transpiring surface and (iv) the stationary phase of wilting when transpiration was reduced to zero level.

While the general trend of variation remained the same under different conditions of experiment, the earlier the period of life cycle, the more marked were the phases of declining transpiratory activity. Fertilisers and varieties affected transpiration mostly during the first phase of high transpiratory activity under relatively high moisture content of soil. When moisture was depleted below a certain critical limit, the individual effects of fertiliser treatment were less discernible.

The efficiency of transpiration (transpiration/dry weight ratio) was usually higher in control than in treated plants. With fertilisers there was a general decline in transpiration. Fertiliser effects at later stages of soil desiccation were rather erratic and less significant than the effect of soil moisture.

Wilting coefficient of soil was more or less similar with the two varieties experimented upon, the range of variation under different conditions being 4.2 to 8.1 in case of Katua and 4.3 to 7.1 in case of Phulwa. Nitrogen fed plants depleted soil moisture to the maximum extent followed by those of Phosphorus fed plants. Potash and PK treated potato reduced the moisture to a lesser extent.

The variation in transpiration have been discussed with reference to varietal characteristics, fertilisers, soil moisture, and atmospheric conditions. A general picture of plants behaviour under depleting soil moisture has been presented.

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*ROLE OF HETEROCHROMATIN

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(Received on August 25, 1949)

I. Heteropyknosis—(a) Heterochromatin and (b) Euchromatin

It is known that some chromosomes or chromosome segments respond to staining during mitosis or meiosis in a different way from the rest of the set and this phenomenon is known as heteropyknosis which signifies difference in density of staining in different segments of the chromosome. The more densely stained segment is called "heterochromatic" to distinguish from the "euchromatic", the rest of the set taken as standard.

Linear differentiation of the extended chromonema is thus revealed in both euchromatic and heterochromatic regions. In the salivary gland chromosomes the heterochromatic regions lying adjacent to the centromeres frequently show a vesiculate type of chromomere in contrast with the compact type characteristic of euchromatic regions. This has not been a useful criterion for revealing the location of intercalary heterochromatic segments in *Drosophila melanogaster*. In induced rearrangements, the nucleic-acid content of a disc and the appearance of its chromomeres will depend not only on the general environment provided within the nucleus but also on its position within the chromosome. Such a position effect might account for the absence of heterochromomeres in regions of salivary gland chromosomes. Alterations in general conditions of the cells may account for the type of flexible heterochromatization. In salivary gland chromosomes the boundary between heterochromatin and euchromatin is variable. Many discs which appear euchromatic in some cells have, in other preparations, the diffuse appearance characteristic of heterochromatin. In meiotic cells the rate of nucleination of euchromatic portions of the distal section of the arm of X-chromosome appears to depend on proximity to heterochromatin.

The suggestion has been advanced that the essential difference between euchromatin and heterochromatin may depend on the proximity of chromomeres with the same nucleic-acid cycle; a heterochromatic segment being one with a high proportion of similar or identical chromomeres. However, in some plants the heterochromatin in different parts of the same nucleus or in different cells at the same stage may present different cytological appearances. Cytogenetic studies on *Drosophila* have revealed that certain position effects depend on the proximity of the locus to a specific portion of the heterochromatic material. For example, the heterochromatic segment which constitutes about one-fifth of the

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left limb of the second chromosome of *Drosophila melanogaster* has been reported during mitosis to be reduced to a single band in the salivary gland nucleus, whereas the bulk of the heterochromatin seen in the salivary gland chromosome is derived from another segment of the mitotic chromosome. In the root tips of *Allium* after fixation, pronounced differential staining was obtained in the heterochromatic regions in the contracted metaphase and anaphase chromosomes. The heterochromatin of the centric regions was found to retain the stain longer than that in other parts of the chromosome. Accordingly, the conclusion was reached that the proximal heterochromatin is of a special kind, essential for the functioning of the centromere.

II. Heterochromatin as Distinguishing Characteristic of Species

The extent of the heterochromatic segment often varies very greatly from one species to another, even within the same genus. Some authors have called the species having longer heterochromatin, megaheterochromatic, while those having smaller amount of heterochromatin as, microheterochromatic. Heterochromatin seems to be relatively inert genetically in most of the forms so far examined. This means that the heterochromatic regions of chromosomes have fewer genes per unit length and these genes seem to be mostly those the phenotypic effects, of which are individually slight. Duplications or deficiencies of heterochromatic regions are likely to affect the viability of the organism much less than duplications or deficiencies of comparable length in euchromatic segments. But this variation is not haphazard and without significance since in the megaheterochromatic species the increase of the heterochromatic regions usually seem to have taken place in a very regular and orderly manner in all the chromosomes. It is an invariable constituent of chromosome and all chromosomes have one or more heterochromatic segments which may be long or short.

Heterochromatic region may arise every time that a minute euchromatic regions undergoes repeated reduplications in the genotype. Harland (1939) found that the same function may be performed in one species by a single gene and in a related species by many. It is perhaps an example of the genetical consequences of this process. Many heterochromatic segments may be found with variations in size. Inversions and other structural changes may break up an originally compact heterochromatic segment into many small ones interspersed among euchromatin. Natural selection and accidental variation seem to have a number of possibilities here. Wharton and White (1943, 1943a and 1943b) stressed that heterochromatin plays an important part in speciation. Mather (1943) studied the function of linkage between 'polygenes' as a basis on which the evolutionary plasticity of a species is founded. He has now reached the conclusion that heterochromatin is made up of polygenes. The formation of new heterochromatic segments, their loss or dispersion and their variation, are all mechanisms whereby polygenes may arise and linkage between them may be created and varied.

(a) ALLOCYCLY

Darlington and LaCour (1940) have suggested that heterochromatic portions of the nucleus differ from other parts of the chromosomes in the timing of the nucleic-acid attachment in relation to the cycle of reproduction and this is called allocyclus. In other words, heterochromatin is allocyclic. It is also known that chromocentres exhibit a consistency in form, number and position that is characteristic for the individual or species. The same segment or chromosome may be visibly allocyclic in one tissue and may have a different allocyclic behaviour in another. Thus allocyclic behaviour is determined by four factors. Firstly, the reactivity of the heterochromatic segment itself and the conditions of the cells. By low temperature treatment heterochromatic segments have been determined which could not otherwise be identified as such. Secondly, two or more heterochromatic segments in the same nucleus or even in the same chromosome often differ from each other besides differing from euchromatin, in their nucleic-acid cycle. Thirdly, heterochromatic chromosomes have been identified of any visible length. They may be located in any part of the chromosome set. Fourthly, certain heterochromatic segments in some species have the property of non-homologous association in the prophase of meiosis or in the pachytene chromosomes. This property is of erratic occurrence and tends to occur in groups of isolated species, rather than at random.

(b) INERTNESS OF THE HETEROCHROMATIC REGION

Since the discovery by Muller and Painter (1932) of genetically inert chromosome segments and their identification with heterochromatic segments, inertness has been found to accompany allocyclus in all ambiguous cases. This inertness manifests itself in two ways—one is that per unit length, heterochromatic segments carry fewer or no genes detectable by sharply alternative effects of different allelomorphs. The other is that deficiencies or duplications for heterochromatic segments have far less harmful effects than deficiencies or duplications for euchromatic segments of the same size. The inertness of heterochromatin may mean that either there are actually few or no genes in it or there are a full quota of genes but the developmental effects of mutation or change in quality in them are difficult to detect. Recent work suggests that the latter alternative is correct.

Caspersson (1939) and his collaborators consider heterochromatin as built up of identical or similar elements or genes. They consider that the greater uniformity of heterochromatin is expressed in the simpler types of proteins.

Darlington and LaCour (1938) have expressed the idea of lesser internal differentiation of heterochromatin by saying that difference between activity and inertness is the difference between high specificity and low specificity.

Thus knowledge of the distinction of heterochromatin is increasing slowly. Information is also being gained about the location and properties of the included genes. The original concept of genetic inertness applied to heterochromatin has been replaced by that of specialized

function. Some workers have suggested that heterochromatin may contain a series of replicated units that serve essentially as modifiers of characters determined by other loci. Other workers have said that heterochromatic genes function primarily in the control of nucleic-acid formation.

(c) HETEROPYKNOSIS AS AN INDEX OF LOCATION OF HETEROCHROMATIN

Heteropyknosis has frequently been mentioned as an index to the location of heterochromatic regions. However, chromosomes that are heteropyknotic in some divisions may condense at a slower rate or at the same rate as the autosomes in other mitoses. If heteropyknosis is accepted as the sole criterion for identifying heterochromatin, the X-chromosome in certain grasshoppers must be regarded as heterochromatic in spermatocytes in which it condenses at the same rate as the autosomes. In the males of certain scale insects one entire haploid set is heteropyknotic in somatic tissues and during spermatogenesis. Obviously heteropyknosis in this situation does not provide an index of genic inertness of the chromosomes involved.

Some chromosomes are entirely heterochromatic or nearly so. A classical example is that of the Y-chromosome of *Drosophila melanogaster* which is essentially inert in the sense that it does not carry genes requisite to normal growth and development, but indispensable because its presence is necessary to ensure fertility in the male. The B-type chromosomes of maize have shown a staining reaction during the resting stage of mitosis which is characteristic of heterochromatin. They are often distributed irregularly at mitosis and undergo alterations in size but they are maintained in the population from generation to generation.

In Sorghum, the B-chromosomes are lost by lagging in the cells of the radicle before seed ripening and in the shoot tissues as they attain maturity. Chromosomes that reach the cells of the anthers and ovaries, however, are maintained regularly. At the second division in the pollen grains, B-chromosomes pass to the generative pole undivided. Following this the vegetative nucleus may undergo a series of additional divisions, presumably as a result of the effect of heterochromatin on the cytoplasm.

III. Chemistry of Heterochromatin

According to P. C. Koller (1943) the nucleus during the resting stage contains a relatively small amount of thymonucleic-acid because at the end of mitosis most of the nucleic-acid charge of the chromosomes is given up. There are chromosome regions, the function of which is the production of ribose nucleic-acid through the formation of histone, which is normally collected and stored during the resting stage in the nucleolus. These chromosomes or chromosome regions are designated as heterochromatic to distinguish them from the euchromatic regions. For the normal functioning of the cell a specific heterochromatic-euchromatic balance is required. The amount of nucleic-acid and its rate of production determine the frequency of division of the nucleus. An incorrect balance between heterochromatin and euchromatin that is, an increase in the nucleic-acid supply, may be very slight, and result

only in a shortening of the resting stage between two divisions. One of the most frequent failures in the mechanism of the division under such conditions is irregular segregation of chromosomes at anaphase, which secondarily leads to a further unbalance and increase in the nucleic-acid supply within the cell. This will be manifested by (1) abnormal chromosome behaviour and (2) by a change in the size and contents of the nucleolus. The excess of the nucleic-acid brought about within a normal cell is due to the fact that heterochromatic regions of chromosomes which are primarily concerned with the nucleic-acid synthesis, can undergo spontaneous mutation and structural change more easily than other parts. It may be probable that the initial change in the nucleic-acid metabolism is brought about by a gene mutation which may be assumed have occurred in the region controlling nucleic-acid supply either directly or indirectly.

According to Mather (1943) there is considerable amount of evidence for considering heterochromatin as internally less differentiated than euchromatin. The reason can be due to the nucleic-acid cycle. During a brief part of the division cycle euchromatic regions are far from uniform along their length. This part is early prophase especially of meiosis, where nucleic-acid has already condensed along the chromosomes but their lengthwise contraction is barely starting. In this short period the chromosomes are distinctly visible and obviously differ from each other in their nucleic-acid charge. Each chromosome shows a distinct reactivity of its own in nucleic-acid synthesis, *i.e.*, it is allocyclic in relation to others because its cycle is shifted in time, relative to that of other chromosomes or because different chromomeres synthesize at different rates or reached different final changes. The giant salivary gland chromosomes of Diptera show the longitudinal differentiation of euchromatic regions better. As mitosis or meiosis proceeds the chromosomes contract enormously by spiralization and loss of proteins. Consequently it is no longer possible to distinguish the individual chromomere. All that a chromosome segment can show is the aggregate effect of its component chromomeres. The cyclic reaction of the chromosomes is generally attributed to synthesis during prophase and breakdown, during telophase of desoxyribose nucleic-acids.

IV. Critical Appraisal and Conclusion

If the view that heterochromatin is made up of elements less differentiated than euchromatin, is accepted then it is to be assumed that these elements are chromomeres and chromomeres of the same type as those found intermingled in euchromatin. The essential difference between the two types of chromatin would then be exclusively in the linear arrangement of chromomeres with the same nucleic-acid cycle. A heterochromatic segment is one with a very high proportion of these similar or identical chromomeres. In *Drosophila* some heterochromatic segment in a salivary gland nucleus agree in having the same type of chromomeres.

Furthermore the type of chromomeres of each heterochromatic segment will not be the same for different segments, thus accounting for the different allocyclic behaviour of two or more segments in a nucleus.

Non-homologous pairing occurs just in those species where two or more heterochromatic segments have a common origin. Thus the allocyclic behaviour can be accounted for by assuming a different linear arrangement of similar chromomeres without any difference in the nature of chromomeres themselves.

The main inference drawn is that heterochromatin acts as a regulator of nucleoprotein metabolism of the cell and, therefore, controls the reproduction of chromosomes. This function is deduced mainly from the consideration of the nucleolus and the disturbances arising in the division of the nucleus as a whole in consequence of excess or deficiency of heterochromatin. Each heterochromatic segment would exercise both a localized and a general specific effect on the conditions of nucleoprotein synthesis in the nucleus often different from non-specific effects of any euchromatic segment of comparable length.

It is, therefore, plausible to venture a prediction that close investigation will reveal very characteristic differences in the action of different heterochromatic segments in the same species and between different species. It may also be quite likely that general differences of a physiological nature may exist between mega and micro-heterochromatic species. Most of the authors who have studied mega-heterochromatic species were interested previously in the phenomenon of non-homologous pairing between heterochromatic segments.

It may be worth mentioning that a comparison between resting somatic nuclei from the same kind of tissue in a number of related species is usually quite sufficient to determine the amount of heterochromatin in a rough manner. In the mega-heterochromatic species the chromocentral masses will be very much larger. Eventually a quantitative index may be fixed to express the amount of heterochromatin in species. Where heterochromatic chromosomes are present in varying numbers in a species, this series exists within the species, so that it will become easier to distinguish between mega-heterochromatic and micro-heterochromatic individuals. This is an unusual situation but an investigation designed to detect slight physiological differences between these individuals might throw considerable light on the more general problem of inter-specific differences in the amount of heterochromatin present.

Lastly it may be concluded that heterochromatin is an important component of the centromeric apparatus. In view of the special function of the centromere in all organisms it would be by no means surprising if a specialized type of heterochromatin somewhat differing in stainability from the rest of the heterochromatin, would participate in the building up of the centromere and thereby it may be more helpful in the differentiation of the evolution of species.

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PROLIFERATION AND SOME OTHER ABNORMALITIES IN THE INFLORESCENCES OF SOME GRASSES

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(Received for publication on September 17, 1949)

I. Introduction

The abnormalities of inflorescences, which form the subject matter of this paper, consist in most cases of vegetative shoots developing in place of spikelets. This phenomenon has been designated differently by different authors. Linnæus (1737, 1759), who found it in *Polygonum viviparum* and some grasses, gave it the name "vivipary". Mattfeld (1920) has also used this term in the same sense, but others (Arber, 1934) have suggested that only the germination of the seed on the parent plant should be regarded as true vivipary and the phenomenon described by Linnæus is better designated as proliferation.

Proliferation is known to occur in several species of grasses. Exo (1916) in his account of *Poa alpina* mentions 25 genera and 45 species of grasses as "viviparous" but Nannfeldt (1940) has shortened the list considerably. According to him "vivipary" occurs regularly only in *Deschampsia* (3 species), *Festuca* (2 species) and *Poa* (4 species). Gustafsson's (1945, 1947)² recent list mentions the following: *Agrostis*

¹. The observations embodied in this paper were made when I was employed at the University of Dacca but the final preparation of the manuscript was completed at the University of Delhi.

². Gustafsson's papers have been the main sources of my information as many of the references were not available to me in original.

stolonifera, *A. tenuis*, *Deschampsia alpina*, *D. caespitosa* (apomictic forms) *D. rhenana*³, *Festuca ovina* (apomictic forms), *F. rubra* (apomictic forms) *Poa alpina* (apomictic forms), *P. arctica*, *P. bulbosa*, *P. pratensis*, *P. herjedalica* (= *alpina* × *pratensis*) and *P. jemtlandica* (= *flexuosa* × *alpina*). In her account of proliferation Arber (1934) has also included *Trisetum flavescens*, *Hordeum murinum*, *Arrhenatherum avenaceum*, *Phleum pratense*, *Andropogon sorghum*, *Cynosurus cristatus*, *Agrostis palustris* and *Lolium perenne*, and Nielsen (1941) has added five more names to the list, namely, *Festuca obtusa*, *Bromus inermis*, *B. purgans*, *Avena sativa* and *Panicum virgatum*. Mudaliar and Sundararaj (1949) have recently reported proliferation in *Pennisetum polystachyum*.

The present account deals with four species of grasses, viz., *Saccolipsis myosuroides*, *S. interrupta*, *Eragrostis nutans* and *Oryza sativa* var. *fatua*. As far as I am aware these have not been previously included in the list of grasses showing "vivipary" or proliferation.

II. Material

Saccolipsis myosuroides and *S. interrupta* are quite common in Bengal. The latter grows in water or near it and is frequent in the vicinity of paddy fields. The first specimen of *S. myosuroides* showing proliferation was collected from Chittagong by the late Mr. S. K. Sen (Curator of the Herbarium, University of Dacca) and the author in October, 1940. Later, proliferating specimens of both species were collected from the Dacca district near Narayanganj, Tejgaon and Tongi. Some plants of *S. interrupta* were transplanted to the Dacca University Botanic Garden where they grew quite well. In November last another trip was made to Tongi and a large number of proliferating specimens of both species were collected. On this occasion and later, living specimens of *S. myosuroides* also were brought and grown in the Dacca University Botanic Garden. Proliferating specimens of both the species were found quite frequently. The phenomenon is a regular occurrence and not a sporadic one.

The other two species are also common in Bengal. Abnormal plants of *Eragrostis nutans* were collected from Tongi in November, 1948 and January, 1949 and some had been successfully transplanted. Specimens of *Oryza sativa* var. *fatua*, an awned variety, were collected at the same time and from the same locality. They were found in wet places in association with *Saccolipsis interrupta*.

III. The abnormalities

The normal inflorescence in *Saccolipsis myosuroides* (Fig. 1) and *S. interrupta* (Fig. 9) is a cylindrical spike-like panicle in which the rachis bears little fascicles of shortly pedicellate spikelets. The inflorescence as well as the spikelets of the first mentioned species are smaller than those of the second.

For the sake of convenience, the abnormal inflorescences of *S. myosuroides* may be classified into three forms. The first form resembles

³. Another species, *D. litoralis*, although not included in the list which he has given in an appendix, has been mentioned by him in the text (Gustafsson, 1945).

PLATE I

Figs. 1-8. *Saccolipsis myosuroides*.

1. Normal inflorescence.
2. Inflorescence with one proliferation.
3. Inflorescence with three proliferating shoots.
4. Inflorescence with a proliferating shoot showing lateral axes bearing spikelets.
5. Abnormal inflorescence with an involucre and reproductive (indicated by arrow) and vegetative shoots at the apex of a naked axis.
6. Abnormal inflorescence similar to that in Fig. 5 but with three nodes separated by long naked internodes.
7. A plant with three normal inflorescences and one similar to those shown in Figs. 5 and 6.

the normal inflorescence in all respects except that it bears, in place of certain spikelets, one or more vegetative shoots, described as bulbils, propagules, or proliferations, which often project quite conspicuously from the axis of the inflorescence (Figs. 2-4). The number and size of these shoots vary. The maximum number so far observed in an inflorescence was five and the longest of these measured about 4.5 centimetres

PLATE I—Contd.



8

9

10

11

Fig. 8.—*Saccolipsis myosuroides*.

8. Inflorescence with a bulbil.

Figs. 9–11. *Saccolipsis interrupta*.

9. Normal inflorescence.

10–11. Abnormal inflorescences with several proliferating shoots.

although the majority were nearly 3 cm. or less. Each shoot consists of a stalk similar to that of a spikelet but two to four times as long, and a short axis which bears near its base a few bract- or glume-like structures and in the upper portion small leaves complete with sheath, blade and ligule. In a shoot measuring 14 mm. in length the axis measured only about two mm. The glume-like structures resemble ordinary bracts in general form but are much larger, their size increasing from base towards apex. The leaves also show an increase in the same direction. In the shoot measuring 14 mm. there were four bracts or glumes, four small leaves and a long tubular sheathing structure at the apex. However, the number of bracts and leaves in a shoot seems to bear no particular

relation to the length of the shoot. The shoots may possess only vegetative organs or bear one or more lateral axes carrying a few spikelets (Fig. 4).

In the second type of abnormality of which only one specimen was available, the shoot appearing in place of a spikelet was a swollen or bulbous structure bearing a few bracts (Fig. 8)⁴. This may more appropriately be regarded as a bulbil. Its form strongly suggests that if detached from the parent plant and placed under suitable environmental conditions, it might have developed into a new plant. This has actually been found to be the case in *Poa bulbosa* (Kennedy, 1929).

The third type of abnormality is a bizarre modification of the inflorescence, showing a pronounced departure from the ordinary type. It consists of a naked axis bearing at its apex a number of large sized bracts forming a sort of involucre (Fig. 5). The bracts may be 2.5 cm. or more in length. From the axils of some of them arise lateral axes, which may be long or short and bear a few spikelets upon them. The shorter ones bear the spikelets along the whole length except for a small basal portion. The longer ones are naked below and show the spikelets in the apical part. Emerging from amongst the bracts are also seen vegetative shoots. A variation of this form of abnormality consists in there being two or three groups of bracts and the associated structures as described above, separated from one another by internodes of considerable length (Figs. 6 and 7).

All the abnormal specimens of *S. interrupta* (Figs. 10 and 11) belonged to the first type described above. The number of proliferating shoots per inflorescence is larger in this species and one inflorescence showed as many as ten shoots (Fig. 11). They were also much larger than those of *S. myosuroides*, the largest being about 5 cm. in length. This difference may possibly be associated with the greater size of the spikelets and the inflorescence in *S. interrupta*.

The abnormalities observed in the other two species, namely, *Eragrostis nutans* and *Oryza sativa* var. *fatua*, also fall under the first form mentioned in connection with *S. myosuroides*. Specimens of *Eragrostis* are noteworthy because of the large number of vegetative shoots seen in a single inflorescence although they are small in size. Fig. 12 shows an inflorescence with more than twenty shoots. In another specimen with a small inflorescence these vegetative shoots were a good deal more conspicuous than the spikelets. In *Oryza sativa* the proliferating shoot was about 2.5 cm. in length in one case (Fig. 13) and had grown to about 10 cm. in another.

IV. The role of proliferation in propagation

It is to be verified whether the shoots developing in the inflorescence in place of spikelets and called propagules or bulbils actually behave as such and give rise to new plants in nature. The possibility cannot be

⁴. As only one specimen was available it was not considered advisable to dissect it. Attempts are being made to collect additional material to study the structure of the bulbil in greater detail.

denied because the shoots consist of nodes and internodes, and rooting at the nodes is a common phenomenon in grasses. As already indicated, the form of the shoot seen in the second type of abnormality described under *S. myosuroides* also strongly suggests such a possibility. Some authors have reported that roots may develop on the shoots while they are still attached to the parent plant. *Poa alpina* (Exo, 1916) and *Festuca ovina vivipara* (Turesson, 1926) are cited as examples of this kind. In the former the roots are already 1-2 cm. long when the bulbils become detached from the parent plant. In *Poa bulbosa* (Kennedy, 1929) in which the bulbils are similar to those of *S. myosuroides* (Fig. 8) they fall off from the inflorescence in summer and germinate in autumn after a resting period of several weeks. Arber (1934), on the other hand, says that under natural conditions proliferated spikelets seldom grow into new plants.

To decide the point experimentally in case of the plants discussed here, a few of such shoots were placed in soil in pots. These remained green for about twenty days after which they began to dry up from the apex towards the base. After about a month they dried up completely. Their ability to remain green for more than twenty days strongly suggests the possibility of their germination and developing into new plants but, further trials are of course necessary to draw a final conclusion.

Pots containing garden soil were placed under inflorescences bearing such shoots to see whether they drop down naturally, and if so, whether they grow into new plants after a time. The observations made so far have given only a negative result. The shoots have been found to persist on the inflorescence even after all the spikelets had withered and fallen. In two plants of *S. interrupta* and one of *S. myosuroides* the shoots remained green for ten to fifteen days on the otherwise bare rachis. They then gradually dried up and shrivelled although still attached to the parent plant. Dead and dry proliferating shoots remaining attached to the parent plants have also been observed in other specimens of *S. myosuroides* and in one of *Eragrostis*.

V. Summary and conclusion

1. Proliferation is a common phenomenon in *Saccolipsis myosuroides* and *S. interrupta* both in the field and in the garden. It was also observed in several specimens of *Eragrostis nutans* and *Oryza sativa* var. *fatua*.
2. In *S. myosuroides* a bulbil-bearing inflorescence was observed. This species shows another form of abnormality in which the inflorescence, instead of being a uniformly cylindrical structure consists of 1-3 nodes separated by long naked internodes. Each node bears an involucre of bracts and a few reproductive and vegetative shoots.
3. Observations on the ability of the proliferating shoots to germinate and produce new plants have so far yielded only negative results.

It seems unfortunate that the term "vivipary" has been applied to a method of reproduction which should properly be included among the various modes of vegetative propagation. This is particularly so because

PLATE II



12

13

- Fig. 12. *Eragrostis nutans*. Inflorescence with more than twenty proliferating shoots (some of these are indicated by arrows).
- Fig. 13. *Oryza sativa* var. *fatua*. Inflorescence showing proliferation.

"vivipary" is in common use as an antonym of "ovipary". It is still more inappropriate to use "vivipary" for those cases in which the capacity of these shoots to germinate into new plants has not been definitely established. The term "proliferation" seems to be more preferable because of its non-committal nature.

I am indebted to the late Mr. S. K. Sen in whose company many of the specimens were collected from Chittagong and Dacca, and, who also identified the plants, to Prof. P. Maheshwari who helped me in writing this account, and to Mr. Q. A. Ahmed (Dacca University) for the collections made in 1948. I should also like to take this opportunity of expressing my sincere gratitude to Mr. V. Narayanaswami (Royal Botanic Gardens Herbarium, Sibpur, Calcutta) who has favoured me with the specific identification of the specimens of *Eragrostis*.

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A PRELIMINARY NOTE ON THE MINIMUM PERIOD OF 'SHORT-DAYS' REQUIRED FOR EARLY HEADING IN PADDY AND ITS APPLICATION UNDER FIELD CONDITIONS

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(Received for publication on October 13, 1949)

The method of altering the time of flowering was initiated by Garner (2) and Garner and Allard (3), who introduced the term photoperiodism to designate the response of plants to the relative length of day and night. Numerous investigators have since then published results of studies of this phenomenon. Chien Liang Pan (1), Hara (4), Sircar (6,7) and Sircar and Parija (8) reported the effectiveness of this method for inducing early flowering in paddy. Saran (5) working on several varieties of paddy concluded that all paddy varieties irrespective of their normal flowering dates can be induced to flower by this method within 60-63 days of germination or at any desired time during their growth period. Saran removed the experimental plants each day to a dark-room at 3 and 5 p.m. In the following mornings at 5 a.m. the plants were taken out in the open. Earing was noticed after 30-33 days of the treatment, when the treatment was discontinued and the plants received normal light along with the control. In the following account the results of experiments to determine the minimum period of 'short-days' required for early heading in paddy and its application under field conditions is briefly described.

Material and Method

Seed and the experimental pots: Uniform seeds from one pure strains 36 BK—a late 'Aman' paddy—were taken. Seeds were sown on 26th May in pots containing well mixed soil from paddy field. Each pot had three seeds. After germination in each pot the seedlings were thinned down to one. Pots showing uniform growth were divided into three experimental sets of 56 pots.

Age of the seedlings: Age of the seedlings was counted from the day they came out of the soil.

Experimental sets: There were three experimental sets, namely sets I, II and III, where seedlings of the age of 30, 60 and 90 days were used respectively.

Treatment: (a) 'Short-days': 'Short-day' treatment was given in each set by removing the plants from open to a well ventilated dark room each afternoon at 3 p.m. In the following morning at 5 a.m. these plants were taken out and placed in the open with the controls.

(b) *Time and duration of the 'short-day' treatment:* In sets I, II and III, the treatment was started on 1st July, 31st July and 30th August and ended on 30th July, 29th August and 29th September respectively.

In each set, after receiving the treatment for 5, 10, 15, 20, 25 and 30 days, a set of 8 plants picked up at random, were removed from the experiment on dates given in column 1 of Table I and were placed in the open along with the control plants and their subsequent growths were carefully watched.

Results and their Consideration

From the results set out in Table I, it can be seen that in all the three sets the plants receiving the treatment up to 10 days flowered with the control on 26th to 29th October—showing thereby that ‘short-day’ treatment up to 10 days has no effect whatsoever in inducing early heading. It is interesting to note in this connection that 10 days of ‘long-day’ treatment was also found by the author (5) to be quite ineffective to delay flowering in paddy.

Plants receiving the treatment for longer periods, *i.e.*, for 15, 20, 25 and 30 days in each of the three sets, however, behaved similarly and came

Table 1 showing the effect of ‘short-day’ treatment on the time of flowering of paddy plants

Period of ‘short-day’ treatment.	No. of days for which the treatment was given.	Flowering duration.	Induced earliness in days.
1	2	3	4
<i>Set I: 30 days old seedlings.</i>			
1st to 5th July	5	28-10 to 29-10	..
1st to 10th July	10	26-10 to 28-10	..
1st to 15th July	15	1- 8 to 2- 8	88
1st to 20th July	20	31- 7 to 2- 8	89
1st to 25th July	25	1- 8 to 2- 8	88
1st to 30th July	30	31- 7 to 3- 8	89
Control	28-10 to 29-10	..
<i>Set II: 60 days old seedlings.</i>			
31st July to 4th August	5	27-10 to 29-10	..
31st July to 9th August	10	28-10 to 29-10	..
31st July to 14th August	15	31- 8 to 1- 9	57
31st July to 19th August	20	30- 8 to 1- 9	58
31st July to 24th August	25	1- 9 to 3- 9	56
31st July to 29th August	30	31- 8 to 1- 9	57
Control	27-10 to 29-10	..
<i>Set III: 90 days old seedlings.</i>			
30th Aug. to 4th Sept.	5	26-10 to 28-10	..
30th Aug. to 9th Sept.	10	26-10 to 29-10	..
30th Aug. to 14th Sept.	15	1-10 to 3-10	26
30th Aug. to 19th Sept.	20	30- 9 to 2-10	27
30th Aug. to 24th Sept.	25	1-10 to 2-10	26
30th Aug. to 29th Sept.	30	2-10 to 3-10	25
Control	26-10 to 28-10	..

to flower within the sets almost simultaneously, *i.e.*, between 31st July to 3rd August, 30th August to 1st September, and 30th September to 3rd October, exhibiting an earliness of about 88-89, 56-58 and 25-27 days in flowering respectively. It may further be seen from the table that a minimum of 15 days 'short-day' treatment is required in each of the three cases to bring about early flowering.

Having ascertained the minimum effective 'short-day' treatment to bring about early heading, an experiment was designed in the following season to study the effect of this treatment given at the seedling stage on the transplanted crop. For this purpose requisite quantity of seeds of 36 BK were sown in pots measuring about 2' in diameter. When the seedlings were 30 days old, the 'short-day' treatment was given for 15 days in the same manner as in the previous experiment, *i.e.*, these pots were removed to a well ventilated dark room each afternoon at 3 p.m. and in the following morning at 5 a.m. they were taken out in the open and were kept with the control pots. The treatment was terminated on 5th July and the treated seedlings, after marking the tillers which received the treatment, were transplanted in a well prepared plot next day, along with the control seedlings. The subsequent growth of the crop was carefully watched. Between 6th-8th August earing was noticed in the experimental crop, in those tillers only which had received the 'short-day' treatment. The treated tillers reached maturity by the middle of September. Whereas other tillers which came up later on after transplanting did not show any sign of heading. These untreated tillers, however, came to flower between 28th-29th October along with the control. Results, therefore, indicate a limited utility of this method in producing an early crop under field conditions at Sabour. Sircar and Parija (9) have also noted considerable variation in the flowering times of the main short and the tillers of rice varieties from Bengal.

Incidentally it may be mentioned that in a few pots of 36 BK, half the tillers in each pot were bagged at 3 p.m. each day in thick bags of black cloth. These bags were taken out at 5 a.m. in the following mornings. It was noticed after 33-36 days of this treatment that the tillers which received this treatment in the various pots came to flower between 2nd-6th of September, whereas the rest of the tillers which received no treatment flowered at the normal time, *i.e.*, between 28th-29th October.

Summary of the Results

In a late 'Aman' paddy at Sabour, Bihar—

(a) 'Short-day' treatment up to 10 days was found to have no effect whatsoever in inducing early heading.

(b) Minimum effective period of 'short-days' to bring about early flowering was found to be 15 days.

(c) There is a limited utility of this method in early crop production under field conditions.

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POLLEN GRAINS OF STERCULIACEÆ

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(Received for publication on November 7, 1949).

There is practically no literature on the form and structure of the pollen grains in Sterculiaceæ. Wodehouse (1935) makes a passing reference to the family in his Master Key, but does not give the description of the pollen grains in any member. So, the writer who has been engaged in the study of the embryology of the family, took up the study of the pollen grains and the present article embodies his observations on 9 genera and 11 species. Fresh pollen grains were mounted according to the methyl-green glycerine jelly method described by Wodehouse (Pollen Grains, New York, 1935, p. 106). The study revealed that the pollen grains of different genera are easily distinguishable from one another.

General Observations

The pollen grains of the different genera show much variation in size, shape, nature of exine, germ pore, etc. In size, they range from 15 to 70 μ in diameter. Usually the range of variation in size among the pollen grains of the same species is less than 5 μ , but in *Dombeya spectabilis* Bojer, associated with the normal pollen grains which measure about 55 μ in diameter, occur stray grains which measure 70 μ or more. Such oversized pollen grains are usually found in hybrids and apomicts. One of the probable causes of their origin is the lagging behind of some chromosomes during the meiotic divisions of the microspore mother cells, resulting in the greater number of chromosomes and larger size in some of the pollen grains. As this phenomenon of lagging behind of chromosomes was commonly observed in *Dombeya*, the abnormal pollen grains might have originated in the above mentioned manner. It was also observed by the writer that though 'fruits' are formed in the plants cultivated in the gardens, they are devoid of seeds. This also shows that the plant is a sterile hybrid. The pollen grains in *Guazuma* show seasonal variations and will be described elsewhere.

The pollen grains show three different shapes : spherical as in *Pterospermum*, *Pentapetes*, *Dombeya*, *Waltheria*, *Guazuma* and *Melochia* ; ellipsoid and lobed as in *Sterculia* ; and triangular and oblatly flattened as in *Helicteres* and *Klienhowia*.

The exine in *Dombeya*, *Pentapetes* and *Pterospermum* shows spine-scent outgrowths. In the remaining genera the exine shows either fine granular thickenings as in *Guazuma* or fine reticulate thickenings as in *Melochia* or coarse reticulate thickenings projecting above the general surface as in *Sterculia colorata* Roxb.

Waltheria indica L. differs from other members of the family in having tetracolpate (rarely pentacolpate) pollen grains, whereas in others they are tricolpate. In *Sterculia* species the germ pores are situated in the middle of deep longitudinal grooves which serve as harmomegathi in permitting volume changes. Hence the pollen grains have a lobed appearance. In *Waltheria*, *Guazuma* and *Melochia*, the germinal furrows are shallow and fusiform. Whereas in all other species the germ pore is round, in *Melochia corchorifolia* L. it is rectangular in outline. In these pollen grains, transverse to the main germinal furrow there occurs a thin rectangular region of the exine extending on either side of the germ pore. This also probably acts as a harmomegathus complementing the main furrow. Such an equipment is in keeping with the rectangular nature of the germ pore. *Dombeya*, *Pentapetes* and *Pterospermum* differ from the remaining genera in the absence of germinal furrows. The germ pores are peculiar in having a collar-like thickening which projects both to the outside as well as inside. A ring-like zone of the exine around each germ pore is specially thin and collapsible, while the remaining exine is thick and rigid. This zone acts as a harmomegathus : in turgid condition of the pollen grain, these regions are fully distended and consequently the pollen grain has a spherical appearance ; in the flaccid condition, they collapse slightly and hence the outline of the grain also changes (Figs. 14 and 15).



Figs. 1—21. Pollen Grains of *Sterculiaceæ*.

Figs. 1 & 2. *Waltheria indica* L. pollen grains in surface view.

Fig. 3. Sectional view of the above (*diagrammatic*).

Fig. 4. *Guazuma tomentosa* Kunth.

Figs. 5 & 6. Two different side-views of pollen grains of *Sterculia colorata* Roxb.

Fig. 7. Sectional view of the above.

Fig. 8. Surface view of the exine (enlarged and *diagrammatic*).

Figs. 9 & 10. *Sterculia foetida* L. top and side-views of pollen grains.

Fig. 11. Face-view of furrow showing germ pore of above.

Figs. 12 & 13. *Melochia corchorifolia* L.

Fig. 14. *Pterospermum heyneanum* Wall (pollen grain in turgid condition).

Fig. 15. *Pterospermum acerifolium* Willd (shrunken condition of pollen grain).

Fig. 16. *Dombeya spectabilis* Bojer.

Fig. 17. *Helicteres isora* L.

Fig. 18. Sectional view of the germ pore of the above (*diagrammatic*).

Fig. 19. *Klienovia hospita* L.

Fig. 20. Sectional view of the germ pore of the above (*diagrammatic*).

Fig. 21. *Pentapetes phænicea* L.

All figures except those marked *diagrammatic*. $\times 700$.

In most genera, the intine is uniform in its thickness and is much thinner than the exine. In *Sterculia*, it is much thicker than in other genera. In *Helicteres*, it is very thick below the germ pore and thin in the remaining region, whereas in *Waltheria* it is thin and protruding in the region of the germ pore and thick elsewhere.

The key below is constructed for the identification of the genera and species on the basis of the pollen grain characters, while the following table indicates the characters of the different plants in a tabular form :

Key

I. Pollen grains spherical.

Pollen grains smooth walled ; germinal furrows present, fusiform in shape.

Pollen grains with four germ pores ;
intine protruding through germ pores

Waltheria indica L.

Pollen grains with three germ pores ;
intine not protruding.

Germ pores rectangular in outline ; exine with fine reticulate thickening

Melochia corchorifolia L.

Germ pores circular in outline ;
exine with fine granular thickening

Guazuma tomentosa Kunth.

Pollen grains with spinescent outgrowths ; germinal furrows absent, harmomegathi in the shape of ring-like zones round germ pores.

Spines prominent ; pollen grains 65-70 μ in diameter

Pentapetes phænicea L.

Table showing the characters of the Pollen grains of Sterculiaceæ

No.	Name of plant.	Average size of pollen grains in microns.	Shape.	No. of germ pores.	Size of germ pores in microns.	Nature of germ pores.	Nature of Exine.	Nature of Intine.
1.	<i>Waltheria indica</i> L. . .	38	Spherical	4	8	R o u n d with thick rim.	Reticulately thickened ; germinal furrow fusiform and shallow.	Intine thin immediately below germ pore and protruding through it, thick in the remaining part.
2.	<i>Melochia corchorifolia</i> L.	50	Do.	3	9 × 7	Rectangular	Exine reticulately thickened ; one main fusiform germinal furrow in the middle of which germ pore is situated ; transverse to it is another thin zone.	Uniformly thin ; not protruding.
3.	<i>Guajuma tomentosa</i> Kunth . . .	15	Do.	3	4	Round . .	Exine finely granular ; germinal furrow fusiform and shallow.	Do.
4.	<i>Pentapetes phoenicea</i> L.	70	Do.	3	8	R o u n d with collar like thickening.	Harmomegathus in the shape of a circular zone around germ pore ; stout spines present on exine.	Uniformly thin.

Table—continued.

No.	Name of plant.	Average size of pollen grains in microns.	Shape.	No. of germ pores.	Size of germ pores in microns.	Nature of germ pores.	Nature of Exine.	Nature of Intine.
5.	<i>Dombeya spectabilis</i> Bojer	55	Spherical	3	7	Round with collar like thickening.	Harmomegathus in the shape of a circular zone around germ pore; stout spines present on exine.	Uniformly thin.
6.	<i>Pterospermum hyneanum</i> Wall	52	Do.	3	6.5	Do. ..	Germ pore and harmomegathus as above, spines not so prominent.	Do
7.	<i>P. acerifolium</i> Willd ..	45	Do.	3	6	Do.	Do. do. ..	Do.
8.	<i>Helicteres isora</i> L. ..	20	Triangular and oblate-ly flattened	3	2	Germ pore of <i>Myrica</i> pattern.	Finely granular ..	Very thick below germ pore; thin in remaining part.
9.	<i>Klienovia hospita</i> L. ..	18	Do.	3	3	Germ pore of <i>Carpinus</i> pattern.	Coarsely granular ..	Uniformly thin.
10.	<i>Sterculia foetida</i> L. ..	40 × 28	Ellipsoid and lobed.	3	Reticulately thickened; germinal furrows deep.	Uniformly thick.
11.	<i>S. colorata</i> Roxb. ..	25 × 25	Do.	3	Coarsely reticulate thickening.	Do.

- | | |
|---|--|
| Spines prominent ; pollen grains 53-58 μ in diameter | <i>Dombeya spectabilis</i> Bojer. |
| Spines not so prominent ; pollen grains 50-52 μ in diameter | <i>Pterospermum heyneanum</i> Wall. |
| Pollen grains 45-50 μ in diameter | <i>Pterospermum acerifolium</i> Willd. |
2. Pollen grains triangular in outline and oblately flattened.
- | | |
|--|------------------------------|
| Germ pore of the <i>Myrica</i> -pattern ; exine with fine granular thickening ; intine thick below the germ pore | <i>Helicteres isora</i> L. |
| Germ pore of the <i>Carpinus</i> -pattern ; exine coarsely granular and intine uniformly thin | <i>Klienhowia hospita</i> L. |
3. Pollen grains ellipsoid and lobed ; germ pores situated in the middle of deep longitudinal grooves.
- | | |
|--|---------------------------------|
| Exine with fine reticulate thickening ; pollen grains longer than broad (40 \times 28 μ) | <i>Sterculia foetida</i> L. |
| Exine with coarse reticulate thickening ; pollen grains as long as broad (25 \times 25 μ) | <i>Sterculia colorata</i> Roxb. |

Discussion

The study of the pollen grains of Sterculiaceæ shows that unlike the pollen grains of Malvaceæ, they differ markedly in the different genera. This variation, however, is not haphazard, but is characteristic of the tribes. Wight (1840) and Hooker (1875) divided Sterculiaceæ into six tribes, Hermannieæ, Buttnerieæ, Dombeyeæ, Helictereæ, Sterculieæ, and Eriolaneæ. The pollen grains of the first two are spherical and smooth-walled, of Dombeyeæ spherical and spinescent, of Helictereæ triangular, oblately flattened and smooth-walled, of Sterculieæ elongated and lobed, and of the last tribe Eriolaneæ not studied so far. The six tribes, therefore can now be defined as follows :

TRIBE I. HERMANNIEÆ : *Waltheria* and *Melochia*. Flowers bisexual ; petals flat ; stamens five, antipetalous and united at base ; ovary sessile ; pollen grains spherical and smooth walled.

TRIBE II. BUTTNERIEÆ : *Guazuma*. Flowers bisexual ; petals concave with strap-shaped appendages ; stamens 1-seriate, placed between staminodes ; ovary sessile ; pollen grains spherical and smooth walled.

TRIBE III. DOMBEYÆ : *Dombeya*, *Pentapetes* and *Pterospermum*. Flowers bisexual, regular, involucre present ; petals 5, asymmetrical and contorted ; stamens in five groups placed between staminodes ; pollen grains spherical and spinescent.

TRIBE IV. HELICTEREÆ : *Helicteres* and *Klienhowia*. Flowers bisexual ; calyx and corolla zygomorphic ; andræcium columnal below and dilated above into a cup, with anthers placed between staminodes ; pollen grains triangular, oblately flattened and smooth walled.

TRIBE V. STERCULIÆ : *Sterculia*. Flowers unisexual or polygamous ; apetalous ; andrœcium columnal or sessile ; anthers clustered or in a ring ; pollen grains elongated and lobed.

TRIBE VI. ERIOLÆNÆ : Flowers hermaphrodite ; petals deciduous ; andrœcium tubular, conical, antheriferous for nearly its whole length ; staminodes absent ; pollen grains not known.

The study of the pollen grains also sheds light on the affinities of genera of disputed systematic position. *Pterospermum*, for example, was placed by Wight (1840) in the tribe Dombeyæ, while Hooker (1875) placed it in the tribe Helicteræ. The pollen grains of *Pterospermum* are spherical and spinescent, showing a close resemblance to those of the other genera of Dombeyæ, namely *Pentapetes* and *Dombeya*. They differ markedly from the pollen grains of Helicteræ (*Helicteres* and *Klienovia*), which are triangular, oblately flattened and smooth walled. The flowers of *Pterospermum* are regular and provided with 5 asymmetrical petals which show contorted æstivation as in Dombeyæ and differ from the zygomorphic flowers of Helicteræ. So the inclusion of *Pterospermum* in the tribe Dombeyæ seems to be more justified.

Acknowledgment

The writer expresses his grateful thanks to Prof. A. C. Joshi for his kind interest in the work and valuable suggestions.

only one ~~Reference~~ ?

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